Behavioural and morphological variation in European grayling, *Thymallus thymallus*, populations

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Academic dissertation

To be presented, with the permission of the Faculty of the Biosciences of the University of Helsinki, for public critisism in the lecture hall 2 of the Viikki Information Center, Viikinkaari 11, on May 21st 2005 at 12 o'clock noon.

Helsinki 2005

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ISBN 952-91-8720-3 (Paperback)
ISBN 952-10-2468-2 (PDF)
http://ethesis.helsinki.fi

Yliopistopaino
Helsinki 2005

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This thesis is based on the following articles:

I Water velocity differently affects aggressive behaviour in lake and river populations of European grayling. *Submitted manuscript.*

II Morphological response to water velocity by European grayling *Thymallus thymallus* from lake and river populations. *Submitted manuscript.*

III A short hatchery history: does it make a difference to aggressiveness in European grayling? Journal of Fish Biology (2004) 65 (Supplement A), 231–239.

IV The effect of hatchery rearing on aggressive behaviour and boldness in European grayling (*Thymallus thymallus*). *Submitted manuscript.*

V Early experience of competitive environment affects aggression syndrome in grayling (*Thymallus thymallus*). *Submitted manuscript.*

Contributions

	I	II	III	IV	V
Original idea	AS, NP	AS, NP	NP	AS, NP	AS
Study design	AS, NP	AS, NP	NP	AS, NP	AS
Data gathering	AS	AS	AS	AS, NP	AS
Manuscript preparation	AS, NP	NP, AS	AS, NP	AS, NP	AS, NP

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Summary

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1. Introduction – main sources of phenotypic variation in nature

Phenotypic differentiation among geographically distinct populations is common in nature (Foster & Endler 1999, Clegg et al. 2002, Simmons 2004). A major challenge in evolutionary biology is to understand the proximate mechanisms generating and maintaining this variation among populations. Several natural processes may result in phenotypic differences between populations. The differences may be adaptive originating from divergent selection pressures acting on heritable traits (Merilä & Crnokrak 2001, Schluter 2001). Through natural selection, inferior phenotypes with lower fitness are selected against resulting in different genetic composition of populations inhabiting different environments. Increasing evidence suggests that such adaptive genetic differentiation may occur very rapidly in nature (Huey et al. 2000, Weitere et al. 2004). Such divergent selection on traits between populations inhabiting contrasting environments may ultimately lead to reproductive isolation and thereby to speciation (Schluter 2001).

Migrating individuals transfer genetic material between populations, and gene flow may therefore constrain adaptive diversification of populations in nature (Hendry et al. 2002, Lenormand 2002, Garant et al. 2005). If the selection pressures are strong enough adaptive differentiation may occur even if moderate amount of gene flow exists (Belliure et al. 2000). Evolutionary divergence of populations can therefore be considered to reflect a balance between diversifying effect of selection and homogenizing effect of gene flow (Lenormand 2002, Postma & Noordwijk 2005).

Phenotypic variation between populations relying on genotypic differentiation may be created also in the absence of selection. Random processes, such as genetic drift, may create genetic differences between populations (Yagami et al 2002). Also mutations may change the genetic composition of a population, although the frequency of mutations is generally quite low (Papadopoulos et al. 1999). In small populations or in populations with short generation time they may, however, have evolutionary consequences (Remold & Lenski 2001, Puurtinen et al. 2004). When phenotypic differences between populations are shown to reflect underlying genetic differences, random processes should not be neglected when considering the sources for this variation. If different phenotypes can be associated with particular environmental characteristics adaptive differentiation may, however, be inferred (Endler 1986). Studies concerning

adaptive population differentiation should therefore be conducted with independent populations originating from different environments, reared and studied in controlled conditions.

Phenotypic differences between natural populations may also result from phenotypic plasticity (Agrawal 2001, Peckarsky et al. 2005). Plasticity gives individual a broader way to respond to the environment (van Tienderen 1991, Agraval 2001) allowing the same genotype to produce a variety of phenotypes in response to different environmental conditions (Komers 1997, Schlichting & Pigliucci 1998). Although plasticity has many ecological benefits (West-Eberhard 1989, Agrawal 2001), costs and limits of plasticity have also been suggested (Tauber & Tauber 1992, DeWitt 1998, Merilä et al. 2004). Such negative effects of plasticity may lead to lower fitness of the plastic organism while producing the same mean trait as a fixed organism. They may also result in inability of the plastic phenotype to produce a most optimal phenotype in the current environment (DeWitt et al. 1998). Plasticity may therefore not always be preferable over adaptive differentiation of the trait (DeWitt et al. 1998). Consequently, selection may promote evolution of adaptive geographic variation in the degree of phenotypic plasticity (Via & Lande 1985, Schlichting & Smith 2002, Sultan & Spencer 2002) leading to different reaction norms, i.e. different sets of phenotypes produced by a phenotype, in different environments (Laurila et al. 2002). Plasticity is regarded to be more beneficial in variable environments than in constant environments where most optimal phenotype may be favoured (Schlichting & Pigliucci 1998).

Finally, the environment experienced by the parents may also contribute to the phenotype of offspring (Einum & Fleming 1999, Meylan et al. 2004). These non-genetic parental effects (Mousseau & Fox 1998, Einum & Fleming 1999) are generally important, for example, for offspring size (Mousseau and Fox 1998) and may therefore also contribute to offspring phenotype.

2. Aims of the thesis

Behavioural traits are regarded to be among the first to undergo changes and evolve under environmental change (West-Eberhard 1989), being therefore very suitable for studying phenotypic differentiation. Salmonid young use aggressive behaviour for obtaining and defending food and feeding territories (Grant 1990, Hughes 1992). Aggressive behaviour may therefore have great influence on their survival and fitness (Chapman 1962, Huntingford & Turner 1987). Costs are also associated with individual aggressiveness, such as energetic costs of performing aggressive acts (Vøllestad & Quinn 2003) and conspicuousness to predators (Jakobsson et al. 1995, Martel & Dill 1995). Consequently, aggressive behaviour is expected to be adapted in a unique way to each environment and it therefore suits very well for studying adaptive differentiation of geographically distinct populations. I therefore chose aggressiveness to study both genetic and phenotypic effects of environment on behaviour of grayling (I, III, IV, V).

European grayling is a spring spawning salmonid species which is widely distributed in Europe (Northcote 1995). In Finland grayling inhabits both lakes and rivers as a resident species. After hatching grayling fry live in small shoals near the shores (Scott 1985, Nykänen et al 2003), but already at about two weeks of age they start behaving aggressively towards conspecifics (pers. obs.). In this thesis I have studied the genetic and phenotypic variation of European grayling (*Thymallus thymallus*) populations in aggressive behaviour (I, III, IV, V), behavioural trait correlations (IV, V) and morphological traits (II). As salmonid fish are under intense hatchery rearing I have also addressed the question on the potential effects of unnatural hatchery environment on aggressive behaviour and behavioural trait correlations.

2.1 Phenotypic and genetic differentiation among lake and river populations

Many freshwater fish species are subdivided into geographically distinct populations inhabiting wide variety of differing environments such as lakes, ponds, rivers and rock pools, etc. A remarkably wide range of biological adaptations to these diverse habitats evolved in morphology and physiology (Weigensberg & Roff 1996, Hoffmann 2000) as well as in

various behavioural traits (Foster & Endler 1999). European grayling is a salmonid species exhibiting diverse life history strategies (Parkinson et al. 1999). Some grayling populations are migratory, migrating to spawning or feeding (Linløkken 1993) habitats, but the majority of Finnish grayling populations complete their entire life cycle in rivers or lakes (Northcote 1995). Local grayling populations are characterized with high genetic divergence across short geographical distances (Koskinen et al. 2001, 2002a) indicating low gene flow between populations (Koskinen et al. 2000). Owing to these geographically distinct populations grayling is an excellent species for studies concerning population level adaptations to local selection regimes. In the studies of this thesis I have used Finnish grayling populations originating from both lakes (Puruvesi, Etelä-Saimaa, Kitkajärvi) and rivers (Lieksanjoki and Iijoki).

Lakes and rivers are rather different environments the most evident differences being water velocity and the distribution of food. These may have consequences for both behavioural (I, III, IV) and morphological (V) traits of individual. I was particularly interested in potential genetic differences between lake and river populations (I, II, V), and how experimentally induced conditions may influence populations from the different environments (I, II, III, V).

2.2 Effects of hatchery rearing

Not only the conditions in nature but also conditions created by humans may cause divergence in phenotypic characters (Huntingford 2004). Stocking of hatchery-reared juveniles is a common and widespread practice for enhancement of declined salmonid populations (Jackson et al. 2004, Madeira et al. 2005). Even 95% of released hatchery fish are predated or die from starvation in the first weeks following the release (Brown and Laland 2001). Although the effects of hatchery rearing have been quite widely studied (e.g. Einum & Fleming 2001, Huntingford 2004), additional knowledge of hatchery effects is clearly needed for improving the hatchery rearing practices and enhancing the low survival of hatchery-reared individuals in the wild (Miller et al. 2004). Captive conditions are considerably different from those in nature (Kohane & Parsons, 1988; Price, 1999). Culturing fish from eggs in such environment may select for different genotypes than would be optimal in the wild (Allendorf & Waples 1995). Captive conditions being so unnatural, also the environmental effects of hatchery rearing may result in different behaviour compared to behaviour of the wild fish (Einum and Fleming 2001, Brown et al. 2003b, Laland et al. 2003, Kelley et al. 2005).

Grayling is threatened in many parts of Europe by over fishing, pollution or changes in physical characteristics in its habitats (Magee 1993, Northcote 1995). Also some Finnish grayling populations have been taken to hatchery to strengthen the declined natural populations with hatchery-reared individuals. Long term effects of hatchery rearing are widely studied (Einum & Fleming 2001 and references therein) but in this thesis I was particularly interested if only one generations rearing may create behavioural differences between hatchery and wild strains of grayling (III, IV). Furthermore, I also addressed a question of environmental effects of hatchery rearing on behavioural traits (III).

3. Lake and river habitats

3.1 Genetic differences in behaviour

Aggressive behaviour, as well as behaviour in general, is found to show adaptive variation among environments (Castro & Santiago 1998, Reinhardt 1999, Vehanen et al. 2000). For example water current in natural environment of many salmonid species has been found to be positively related to aggressiveness of individuals (Ferguson & Noakes 1983, Gibson 1983, Puckett & Dill 1985, Swain & Holtby 1989, I, III, V). River-dwelling species appear to be aggressive (McNicol & Noakes 1984) defending territories against conspecifics (Fausch 1984). Fish occupying lacustrine habitats are instead nomadic, move in response to food availability (Erkinaro et al. 1998) and show only little agonistic behaviour towards conspecifics (Noakes 1980, Biro et al. 1997). This was also the finding in my thesis where I found higher aggressiveness in river grayling compared to lake-dwelling grayling in three different

experiments (I, III, V).

Distribution of food is presumably different between lake and river habitats and it could also explain my finding of different aggressiveness between lake and river grayling (I, III, V). In rivers food floats from upstream being both spatially and temporally predictable. Such resource distribution makes it energetically defendable (Grand & Grant 1994, Bryant & Grant 1995, Goldberg et al. 2001) and allows feeding by burst swimming attacks to catch prey items floating by in the river channel (Metcalfe et al. 1997). Furthermore, fast-flowing water makes it more difficult to catch passing food particles, reducing the rate of energy acquisition (Metcalfe et al. 1997). Consequently, occupying an energetically profitable feeding territory with appropriate water flow may be of vital importance in river habitats (Maher & Lott 2000). In lakes, invertebrate food resources occur in spatially and temporally unpredictable patches (Allen & Russek 1985, Grant & Noakes 1988). Foraging in group may be more profitable in exploiting such aggregated and unpredictable food patches (Grant & Noakes 1988, Bryant & Grant 1995, Ryer & Olla 1995, Ryer & Olla 1998, Goldberg et al. 2001, see also V). Consequently, my consistent findings (I, III, V) showing higher aggressiveness in river grayling compared to lake grayling may suggest for adaptive divergence which may result from both different water current and/or food distribution in these environments.

Individuals within a population commonly vary in their behaviour (Wilson 1998, Drent et al. 2003). These differences may be consistent over different contexts, such as aggressive behaviour during feeding and under predation threat (Huntingford 1976), resulting in individual personalities or behavioural types (Budaev 1998). Such trait correlations may result from genetic links among traits (Sokolowski 2001, van Oers et al. 2004) or owe to some underlying physiological constraint, for example an energy allocation trade-off, that is difficult to decouple or modify over evolutionary time (Sih et al. 2003, 2004a). In such case, behavioural characteristics may not be free to evolve independently from each others (Sokolowski 2001, van Oers et al. 2004). A central prediction of such tight trait correlations is that the traits should be similarly related to each other both within and between different populations (Bell 2005). These tight correlations may result in expression of the trait that is of little adaptive significance or that appears maladaptive in the present context (Price & Langen 1992). It has, however, also been argued that behavioural syndromes might be adaptive and their form could thus evolve (Price & Langen 1992, Cheverud 1996, Wilson 1998). In such case different combinations of behaviours should be favoured in different environments (Koolhaas et al. 1999, Sih et al. 2004a, Bell 2005).

In my thesis I addressed a question whether behavioural syndrome may be under selection and therefore different in geographically distinct populations (IV, V). I detected the association between aggressiveness and boldness, i.e. aggression-boldness syndrome to be similar in two replicate populations (IV). Less aggressive individuals appeared also less bold. This gives indication of rather similar selection pressures acting in these two populations resulting in no need to react differently in different situations.

I also investigated aggression syndrome in grayling, i.e. individual aggressiveness in basic and competitive situation. I found that this behavioural relationship was positive and similar in two populations (V). It appeared, however, that this behavioural association was affected by rearing environment in the river fish but not in the lake fish (V). This was indicated by higher aggressiveness in competitive situation in river grayling compared to that of lake-dwelling grayling with similar basic aggressiveness when the fish had been reared in environment where aggressive defence of territory is emphasized. This result gives further support for different food acquisition tactics in lake and river environments. The detected population level difference in ability to alter the behavioural syndrome as a response to prevailing environment (V) may be related to genetic differences between the two populations. My results therefore suggest that, given the link between behaviours, the correlations between behaviours may show adaptive divergence in different environments (IV, V). Owing to the low number of populations I was able to use in each study, I cannot, however, totally exclude the possibility of random drift creating divergence in behavioural syndromes between populations (Yagami et al 2002).

3.2 Genetic differences in morphology

Body morphology of an individual has great importance for its performance in prevailing environment (Arnold 1983). Therefore, in addition to behavioural differences between geographically distinct populations, also morphological differences are common (Riddell & Leggett 1981, Nicieza 1995). In fishes, there appears to be a clear relationship between shape and function, body form affecting the swimming performance of individual (McGuigan et al. 2003). Accordingly, morphological divergence of salmonid populations (e.g. Crossin et al. 2004) has usually been attributed to local adaptation (Pakkasmaa & Piironen 2001, McGuigan et al. 2003).

Body morphology has great functional significance in fish (Andraso 1997, Svanbäck & Eklöv 2004). Owing to different hydrological environment of lakes and rivers, differences in body morphology may be expected in populations inhabiting these environments (McLaughlin & Grant 1994, Schaefer et al. 1999, Hendry et al. 2000, Allouche & Gaudin 2001, Hendry et al. 2002). I was therefore also interested in morphological differences between lake and river grayling (II). I conducted an experiment where grayling from two lake populations (Puruvesi and Kitkajärvi) and two river populations (Iijoki and Kemijoki) were reared in low and high flow in outdoor experimental channels. After one month rearing period lake and river fish could be separated to their own groups based on their morphological characteristics (II). The river fish appeared more slender than the lake fish (II). Slender body may be reasoned to be important in reducing drag when swimming in flowing water and river environment may therefore favour such body shape in grayling. Furthermore, caudal peduncle area was detected to be deeper in river fish compared to that of lake fish. This may also relate to differential swimming demands in these environments as deep gaudal peduncle has been shown to facilitate swimming performance in high water flow (Hawkins & Quinn 1996). The fish used in this experiment were reared under similar hatchery conditions before experimentation and my finding therefore suggest for genetic differentiation in observed morphological differences between lake and river populations.

My study also revealed significant population level differences in morphological traits as the populations could be discriminated from each other by their body morphology (II). These differences may result from divergent selection pressures for morphological traits acting in population level, but also genetic drift and random events (Koskinen et al 2002b) may have affected the differentiation of these geographically distinct grayling populations. It was, however, clear that populations from same habitat resembled each other which may reflect adaptive genetic divergence of morphological traits between lake and river grayling.

3.3 Phenotypic plasticity in behaviour and morphology

Although plasticity is generally considered to be beneficial for individual allowing for better phenotype-environment match across environments (Van Tienderen 1991, Agraval 2001) plasticity has also suggested being costly for an individual (DeWitt et al. 1998, Agraval 2001). Owing to costs and limits of plasticity (de Witt et al. 1998) plastic traits have been suggested to be selected against in environments where they are not needed (Price et al. 2004). Consequently, environments which are constant (or continuously changing) may favour one phenotype that produces best fitness in prevailing environment instead of maintaining plasticity in traits. In temporally and spatially variable environments the trait optima may vary (Dall et al. 2004) and in such conditions phenotypic plasticity is recognized to be an important mechanism of adaptation (Mangel 1991, Pigliucci & Schlichting 1995, Schlichting & Pigliucci 1998).

River-dwelling grayling have been detected to occupy habitats with increasing water velocity as they grow and their hydrodynamic potential increases (Nykänen & Huusko 2003). Already at three months of age grayling juveniles are mostly found in or near the main channel of the river (Sempeski et al.1995) inhabiting rather swift water current areas (Mallet et al. 2000). Also seasonal variation in preferred water velocities has been detected (Mäki-Petäys et

al. 2000). Lake-dwelling grayling, in contrast, inhabit still water with no clear current through their whole life (Sundell et al. 2001). Consequently, in addition to higher water velocity in general, variability in water velocity may be higher in rivers than in lakes (Lytle & Poff 2004). The ability to adjust aggressiveness to different water currents may therefore be of greater importance for river grayling than for lake inhabiting individuals. I addressed this question by studying the phenotypic plasticity of aggressive behaviour in lake and river grayling (I, V). I tested the aggressive behaviour at low and high water velocities in aquaria. In line with the hypothesis, the lake fish did not respond flexibly to different current conditions having similar aggressiveness in high flow and low flow, whereas river fish increased their aggressiveness in response to higher water current (I). Higher flexibility of aggressiveness in river fish compared to that of lake fish may thus represent an adaptation for more variable flow conditions in their natural environment. I did not measure any fitness traits of individuals and may therefore not tell if the detected difference in plasticity owes to costs of plasticity (de Witt et al. 1998). Their inability to behave aggressively in high water current may also owe to some other constraint. For example inferior morphology (II) for swimming in current might constrain aggressive behaviour of lake fish in high water velocity (Taylor and McPhail 1986, Drucker & Laurel 2003).

In addition to single behavioural traits also behavioural syndromes have been suggested to be affected by environmental conditions. Early experiences of individuals are hypothesised to alter behavioural associations (Stamps 2003, Sih et al 2004a), but this hypothesis has not been explicitly studied. In my thesis I aimed at studying the effects of competitive environment during early life on aggression syndrome, i.e. the association between basic aggressiveness and aggressiveness in competitive situation (V). I was also interested in whether this effect is similar in populations originating from lake and river environment. The level of positive association between basic aggressiveness and aggressiveness in competitive situation was affected by early experience on competition, but only in river population (V). Such effect of rearing environment on aggression syndrome was not detected in lake-dwelling grayling (V). The river fish reared in environment where the need for competing for food was higher appeared to use higher aggressiveness in competitive situations than the fish having similar basic aggressiveness but reared in non-competitive environment. Consequently, it was the level of an individual's aggressiveness in the competitive situation that tended to be affected by previous rearing environment in river fish. It thus appears that genetic background of population may influence the outcome of early experiences in behavioural relationships. My results conform to the suggestion that the experiences during early life may affect subsequent aggression syndromes, and that certain plasticity is expected such that individuals may consistently shift their aggression levels depending on conditions (Stamps 2003, Sih et al 2004a). The detected population level difference in this ability (V) to respond to rearing environment may be related to genetic differences between two populations. The effect of early experiences on behavioural syndrome thus appears to be affected also by genetic background of individuals.

Phenotypic plasticity in response to water velocity is commonly recognized in morphological traits of individuals (Pakkasmaa & Piironen 2001, Imre et al. 2002, Proulx & Magnan 2004). In my thesis, I studied if morphological plasticity may be different in lake and river populations (II). I hypothesised the plasticity to be higher in rivers than in lakes owing to differently variable water velocities in these environments. When I experimentally manipulated the water velocity of the rearing environment grayling fry reared in low and fast water currents developed differences in their shape (II). River-originating grayling tended to have shorter pectoral fins and caudal peduncle in high water flow, whereas the middle body elongated in high flow compared to low flow. Shortening of pectoral fins reduces drag (Drucker & Laurel 2003) and it could therefore be energetically more profitable to have shorter pectoral fins in high water velocity. Streamlined body appears beneficial for sustained swimming in high flow (Taylor & McPhail 1986). Therefore, the observed differences in middle body and gaudal peduncle area in river fish reared in low

and high water flow may also indicate different swimming demands in different flow regimes.

As expected, the effect of water velocity on morphological traits appeared clearer in river fish, whereas such plasticity was lacking in lake fish (II). This may indicate higher capability to flexible responses on different water flows in river fish compared to lake fish. This result gives further support to the suggestion of adaptive difference in phenotypic plasticity between lake and river populations. It is in line with my behavioural studies where river-originating grayling had higher plasticity in their aggressive behaviour (I) and aggression syndrome (V) than the lake-originating grayling.

4. The effects of hatchery environment on behaviour

4.1 Genetic effects

In earlier studies where the genetic effects of hatchery rearing on individual behaviour have been studied the fish have often been maintained in hatchery for several generations (Swain & Riddell 1990, Berejikian et al. 1996, Fleming & Einum 1997, Hedenskog et al. 2002, Metcalfe et al. 2003, Petersson & Järvi 2003). However, already one generation's hatchery rearing has been detected to generate divergence in predator avoidance behaviour of hatchery and wild brown trout (Álvarez & Nicieza 2003). In Álvarez & Nicieza's (2003) study, as in many earlier studies, the hatchery and wild fish originated from different populations and the detected divergence may therefore have reflected population difference, not the effect of hatchery rearing per se. I was interested in the effect of such short term hatchery rearing on aggressive behaviour and in my studies I have used grayling populations maintained in hatchery only for one generation. For studying the genetic effect of hatchery rearing I used separate populations of grayling and their corresponding hatchery strains (III). I found that hatchery rearing for only one generation decreased aggressive behaviour of grayling fry (III). Both hatchery and wild fish were reared in identical conditions and the detected differences are therefore most likely of genetic origin.

Hatchery rearing often selects for higher boldness owing to the lack of predators in hatchery environment (Sundström et al. 2004 and references therein). Boldness of individuals has also been detected to correlate with individual aggressiveness (Riechert & Hedrick 1993, Sundström et al. 2003) and therefore my finding of hatchery grayling being less aggressive than their wild counterparts (III) raised a question if boldness would in fact decrease during hatchery rearing. I therefore studied genetic effects of hatchery rearing on aggressiveness and boldness of grayling in an additional study (IV), where I was also interested in the individual level association between these two behaviours, i.e. aggression-boldness syndrome (Sih et al. 2004a). Contradictory to the results of my earlier study (III), I found aggressiveness of hatchery fish to be higher than that of wild fish (IV). A similar positive aggressiveness-boldness syndrome was, however, detected in both hatchery and wild fish (IV) which is in line with the suggestion that aggressiveness and risk taking are correlated characters (Höjesjö et al. 2002). Although the boldness of hatchery fish was only indicatively higher than that in wild fish (IV), the detected behavioural syndrome between these two behaviours suggests that these characters change in synchrony. My result suggests that although hatchery rearing may have a genetic effect on aggressiveness of individual the aggression-boldness syndrome is not affected by hatchery rearing. Owing to the lack of predators the intensity of selection towards traits associated with avoiding and/or escaping predators has been suggested to be limited in hatchery (Einum & Fleming 2001, Huntingford 2004). However, my results suggest that even in absence of direct selection towards boldness, it may ultimately change owing to link between aggressive behaviour and boldness of individual.

The results of the two studies (III, IV) performed in different years studying the genetic effects of hatchery rearing were contradictory. Hatchery fish were detected to be more aggressive than wild fish in one study (IV) but less aggressive in the other one (III). One population, originating from the same hatchery stock was used in both of these studies. The divergent results of these studies therefore suggest for either selection or some

environmental factor(s) resulting in different behaviour in different years. These may both owe to year specific rearing and environmental conditions. One generation in hatchery is quite short time for selection to function. Such rapid change is, however, suggested to be generated during early life stages, when high non-random mortality may result in a change in the frequencies of behavioural phenotypes in a short time (Glover et al. 2004). In my studies the selection directed to aggressive behaviour seems not to be directional as patterns of aggression were different in different years. We did not record the boldness of individuals in the first study (III) study, but it would have been very interesting to know if boldness of hatchery fish was lower than that of wild fish as suggested by the link between aggressiveness and boldness at individual level (IV).

4.2 Environmental effects of hatchery rearing

The environmental factors in hatchery, that have most often suggested to diverge aggressiveness of fish, are high rearing density (Caballero & Castro-Hdez 2003, Sundström et al. 2003), feeding in excess to one predictable place (Grant & Guha 1993, Grand & Grant 1994) and lack of predators in hatchery (Fernö & Järvi 1998). As hatchery reared salmonids in Finland are often stocked to the wild at the age of one to two years (www.rktl.fi), there is potential for great environmental effects of hatchery conditions to affect the subsequent behaviour. Common conditions have recently been shown to converge the trophic morphology of genetically different Arctic charr (*Salvelinus alpinus*) populations (Alexander & Adams, 2004). I therefore addressed the question if the environmental effect of hatchery may also result in convergence of different aggressive behaviour in hatchery and wild grayling. I reared the hatchery and wild originating fish which had been detected to be different in their aggressiveness, for one year in common hatchery conditions (III). Aggressive behaviour of hatchery and wild grayling did not, however, converge during one-year rearing in hatchery conditions (III). It is interesting that feeding conditions in hatchery, having such a large effect on aggressive behaviour (Castro & Santiago 1998), do not result in similar behaviour of hatchery and wild fish. The environment during early life stages has been suggested to have an especially strong affect on subsequent behaviour, which may not be easily modified during later life (Martin 2005 and references therein). It is therefore possible that after early life when the personality of individuals is shaped, aggressiveness may not be changed easily. It is also possible that a year was a too short time for aggressiveness to converge. This would be in line with Álvarez & Nicieza's (2003) suggestion that the behaviour of brown trout in their study was more affected by selection than by experience of hatchery conditions.

5. Conclusions

Owing to repeated findings in this thesis, I suggest adaptive divergence in behavioural and morphological traits between lake and river grayling. Most of the earlier studies, concerning behavioural differences of salmonids inhabiting lake and river habitats, have compared different species, e.g. lake charr and brook charr (Ferguson & Noakes 1983, McNicol & Noakes 1984, Biro et al. 1997), or migration forms of salmonids that spend only a part of their life in lakes or rivers, e.g. Atlantic salmon (*Salmo salar*, Gibson 1983). My studies with resident lake and river populations of European grayling give more reliable evidence of adaptive origin for behavioural differences in lake and river environments.

One of the main themes in this thesis was to study genetic and environmental effects of prevailing environment on behavioural trait syndromes. Behavioural syndromes relate to individual personalities (Bouchard & Loehlin 2001), which are suggested to have different coping strategies in nature (Koolhaas et al. 1999, Sih et al 2004b). To get a more realistic picture on individual behaviour and its evolution, associated behavioural traits should be studied together as also behavioural associations may reflect the adaptation of individuals to prevailing environment. It could also be advisable to have more adaptive perspective on the studies concerning behavioural syndromes and study

the nature and changes of correlation itself instead of just studying which individual behaviours may be correlated and whether such correlations exist in different populations of same species. In my thesis I found that early environment had a different effect on behavioural syndromes in lake and river grayling (V). Consequently, both genetic background of the population and environmental conditions during early life affected the subsequent relationship between basic aggressiveness and competitive aggressiveness in grayling. Studies on the behavioural syndromes represent a new approach on behavioural ecology and most certainly give a broader picture of individual behaviour and adaptive variation of behaviour. More work is clearly needed for studying the behavioural syndromes and their nature but the studies of the present thesis (IV, V) give some information about mixed effects of genes and environment on behavioural syndromes.

Human activities are altering the environment in many profound ways and such human-changed environments may pose evolutionary novel challenges for wild individuals. Owing to human effects the ability to invade new environments may become more important for population persistence (Kawata 2001). Consequently, the ability to respond plastically to environmental changes may be even more important for survival and fitness of individuals in future. According to the results of my studies, lake and river individuals differed in their behavioural and morphological plasticity. Lake-dwelling grayling were found to have lower plasticity in their responses to water velocity than the river grayling (I, II), which represents an adaptation for variability of water flow conditions in their natural environment. This result may also have adaptive significance in natural populations as it may suggest for inferior capability of lake individuals to invade and colonize new habitats in case their old environment is lost or changed.

The results of the studies included in this thesis have several applied aspects. Survival of hatchery fish had often been detected to be very low after stocking to the wild (Arias et al. 1995, Fleming et al. 2000, Einum and Fleming 2001, Borgstrøm et al. 2002). This has been suggested to owe mainly to different behaviour of hatchery fish compared to that of wild individuals (Einum & Fleming 2001). In my studies hatchery and wild strains of grayling were detected to differ in their aggressive behaviour (III, IV). The divergence between hatchery and wild strain was, however, different in consecutive years. Low aggressiveness of hatchery fish (III) may result in competitive advantage of wild fish and lead to low survival of hatchery reared individuals (Miller et al. 2004, Saloniemi et al. 2004). There is also another view suggesting that less aggressive individuals can be more successful in heterogeneous natural habitats (Höjesjö et al. 2002). Evidence, however, shows that highly aggressive hatchery individuals may also out-compete the wild individuals (Largiader & Scholl 1995, McMichael et al. 1999, Einum & Fleming 2001), which may ultimately change the genetic composition of original population in the wild (Weber & Fausch 2003, but see Koskinen et al. 2002b, Susnik et al. 2004, Madeira et al. 2005). Therefore a short-term fitness of highly aggressive hatchery individuals may be high, but in the long run they may not be able to cope with natural conditions. Highly aggressive hatchery individuals may not, for example, be able to optimally cope with predators as aggressiveness appeared to correlate with boldness towards predators (IV). High aggressiveness of hatchery individuals may therefore eventually have a lowering effect on their fitness.

May the aggressiveness of hatchery originating fish be higher or lower than that of wild fish, it may not be at the most optimal level for survival in natural conditions. Increasing concern on the genetic differentiation of hatchery and wild stocks has resulted in attempts to increase the genetic composition of hatchery stocks by enhancing the hatchery stocks with new material from the wild. Such investment is most certainly positive and may result in hatchery reared individuals, which are phenotypically more similar with their wild counterparts.

Early experience on environment was shown to affect the subsequent behaviour of individuals (V). Consequently, in addition to genetic effects of hatchery rearing also the environmental effects of hatchery environment may induce behavioural differences between hatchery and wild fish (Olla et al. 1998). More complex and

enriched, i.e. more natural, environment has been suggested to reduce such environmentally induced effects and increase the survival of hatchery reared individuals after stocking to nature (Berejikian et al. 2000, Einum & Fleming 2001). Rearing conditions in hatchery would definitely deserve more attention in attempts to improve the post-release survival of hatchery reared individuals.

In the studies of my thesis, I found population level differences in both behavioural (I, V) and morphological (II) traits of grayling. Especially the differences between lake and river fish suggest that it could be advisable to use fish originating from the same population in the stocking practices especially when the aim is to support the original population. Such procedure would presumably increase survival of the stocked individuals in the natural environment. Furthermore, owing to environmental effects of early environment on subsequent behaviour (V) and on morphology of individuals (II) it might be preferable to use eggs or first feeding fry for stocking practises rather than fish of later life stages (but see III). Selection may, however, occur already during the egg stage and therefore planting the eggs may not completely protect the hatchery individuals from phenotypic differentiation. It may still prevent the potential additional changes of hatchery environment (V) and therefore be a relevant alternative for stocking the individuals at later age.

When individuals are reared in artificial hatchery conditions it must be kept in mind that the effects of hatchery rearing on individual phenotype can not be avoided. Furthermore, owing to behavioural trait correlations hatchery rearing affects individual personality as whole, not only some traits of individual. Although the progeny of wild parents may not be very well adapted for the hatchery conditions, they would most certainly do better when released into the wild. Catching wild individuals and rearing their offspring in hatchery environment is, however, a bit questionable, as their reproduction could be much more effective in the wild. Consequently, when supportive stocking is a management option, it should be seriously considered whether stocking of hatchery reared individuals does actually do more harm for wild population than support its natural reproduction.

6. Acknowledgements

First and most I would want to thank my supervisor Nina Peuhkuri who patiently guided me through this journey. I have learned a lot during this project. Thank you for always being available when I needed your advice or support. Your passion on science inspired me to move to Enonkoski every summer with renewed enthusiasm. You really taught me how to make good science, which I am very thankful for.

I also want to thank Saimaa Fisheries Research and Aquaculture for providing exellent working facilities and fish for the experiments. Pasi Arkko, J-P Turkka and Veli Luostarinen deserve extra thanks for help with the fish and experimental set-ups.

Anssi Laurila and Erik Petersson reviewed this thesis and their constructive comments on earlier version of this thesis were very valuable.

I sincerely thank Esa Ranta for financing a large part of this work. Esa gave me an opportunity to work in the Integrative Ecology Unit, IKP, in a company of nice and inspiring people. Thank you fellows for creating a very friendly and comfortable atmosphere; it has always been pleasant to come to work. I will not forget the memorable moments that I have spent on- and off-work with you.

IKP girls deserve extra thanks for many enjoyable conversations at their office. Popping into your room has been very essential escape from reality for me during some oppressive moments of this project.

I also want to thank Katja and Anna-Liisa for help and advice concerning bureaucracy and practical things of this process. I could always count on your help, which made the last phases of this work less stressful for me.

All staff at our department is thanked for creating a pleasant atmosphere to work in. I especially want to thank the Metapopulation Research Group people, most of all Marjo and Anna-Liisa, for “honorary membership” and invitations to your leisure activities. Thanks for many delightful moments.

Friends from my student days, Tiina, Teresa, Minna and Sara, thank you for nice and inspiring time I spent in Oulu with you. Those times had a significant role in my decision of starting PhD-studies.

My whole family has had amazingly strong faith in me. Thank you for that! I especially want to thank my parents for all support during the years.

Last I want to thank Ilkka for your love and support. I especially want to acknowledge your patience in the final phase of this work.

The funding for this research came from the NCoE EcoClim (Nordic Ministry Council), Finnish Academy (to prof. Esa Ranta), Jenny and Antti Wihurin rahasto, Kemira Oyj:n säätiö, Elma, Eino ja Veikko Jumppasen säätiö, Oskar Öflunds stiftelse, Suomen luonnonsuojelun liitto and Chancellor of Helsinki University.

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